Methods for estimating sperm whale abundance from passive acoustic line transect surveys*

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1. Introduction

We take the linking of clicks from a survey (or transect) into click segments "known" to come from the same whale, as given. It may be that more than one segment comes from the same whale, but this we do not know. For the moment, we assume that whales occur only in a 2-dimensional plane.

Figure 1 shows an example of the kind of data to be used. Note that the angles (bearings) in this figure are 90^o larger than the angles used below: in the figure 0^o is directly ahead and 90^o is abeam, while in the development below, -90^o is directly ahead and 0^o is abeam.

[Figure 1 about here.]

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2. Full likelihood approach

2.1 *Bearing observation model*

The observed data are actually pairs of arrival times of clicks at the two-element acoustic array. The observed angle of a click from the acoustic array axis is calculated from the difference Δt, between the arrival times at the first and second hydrophones of the click. If the source is sufficiently far from the array, then the angle is well approximated by $b = \cos^{-1}\left[\frac{c\Delta t}{d}\right]$, where c is the speed of sound in water (taken as constant) and d is the distance between the hydrophones. (This equation treats the lines from each hydrophone element to the click as being parallel - see Figure 2.)

[Figure 2 about here.]

The position the animal making the click can be inferred from a sequence of two or more clicks. We assume animals are stationary while within detectable range (can relax this assumption later). Let (x, y) be the location of the animal in Cartesian coordinates, with x being the along-trackline direction. Because of the motion of the towed array (and other things - like bending/slowing of sound in water?), the bearing is observed with error and hence the position is inferred with error. Let $f_b(b \mid t, x, y, \underline{\kappa})$ be the probability density function for the measured bearing b, given the source of the clicks, (x, y), the arrival time t of the click at the first hydrophone and the vector of parameters of this function, $\underline{\kappa}$.

Suppose that clicks and bearings are observed for I click segments, the ith of which contains C_i clicks. Assuming that the b_{ic}s $(i = 1, \ldots, I; c = 1, \ldots, C_i)$ are independent, the probability density function for the measured bearings $\boldsymbol{b} = \{b_{ic} : i = 1, \ldots, I; c = 1, \ldots, C_i\}$ given the click times $\boldsymbol{t} = \{t_{ic} : i = 1, \ldots, I; c = 1, \ldots, C_i\}$ and the locations of the sources of the I observed click segments, is

$$
\begin{aligned}
f_{\boldsymbol{b}}(\boldsymbol{b} \mid \boldsymbol{t}, \underline{x}, \underline{y}, \underline{\kappa}) &= \prod_{i=1}^{I} \prod_{c=1}^{C_i} f_b(b_{ic} \mid t_{ic}, x_i, y_i, \underline{\kappa}) \\
&= \prod_{i=1}^{I} f_{\underline{b}}(\underline{b}_i \mid \underline{t}_i, x_i, y_i, \underline{\kappa}) \qquad (1)
\end{aligned}
$$

where $\underline{x} = (x_1, \ldots, x_I)$, $\underline{y} = (y_1, \ldots, y_I)$. For example, if the error in observing the true bearings from an acoustic array moving at speed v along the trackline a von Mises distribution with mean equal to the true bearing $\theta(x_i, y_i, t_{ic}) = \tan^{-1}\left[\frac{x_i - vt_{ic}}{y_i}\right]$ and concentration parameter κ independent of $\theta(x_i, y_i, t_{ic})$, this pdf is

$$
f_{\boldsymbol{b}}(\boldsymbol{b} \mid \boldsymbol{t}, \underline{x}, \underline{y}; \kappa) = \prod_{i=1}^{I} \prod_{c=1}^{C_i} \frac{1}{2\pi I_0(\kappa)} \exp\left\{\kappa \cos\left[b_{ic} - \theta(x_i, y_i, t_{ic})\right]\right\} \qquad (2)
$$

where $I_0(\kappa)$ is a modified Bessel function of the first kind and order zero.

Considered as a function of the unknown locations $\underline{x}$ and $\underline{y}$ and the parameter vector $\underline{\kappa}$, Equation (1) (or the special case of Equation (2)) is a likelihood from which the sources of the click segments $(\underline{x}, \underline{y})$ can be estimated.

If the standard deviation of the observed angle, b_{ic}, depends on the true angle, $\theta(x_i, y_i, t_{ic})$, the concentration parameter κ may need to be formulated as a function of the true angle.

Lenth (1981) developed similar maximum likelihood methods for the estimation of the location of radio-tagged animals and Guttorp and Lockhart

(1988) extended his model to incorporate a Bayesian approach. The latter in particular may be worth exploring further for estimation of click location from passive acoustic surveys.

2.2 *Click production model*

Typical sperm whale clicking behavior has two states: (a) silence while near and on the surface (state a for $a$bove) and (b) frequent clicking while at foraging depths (state b for $b$elow).

If we discretize the click production process by dividing time into intervals indexed by $j = 1, \ldots, J$ then process can be modelled as a two-state discrete hidden Markov model. The model assumes that transitions between states happens only between intervals, not within intervals. It is as follows:

(i) Let $\pi_b(m; \underline{\lambda})$ be the probability density function (pdf) for the number of clicks m in an interval (with parameter vector $\underline{\lambda}$)), given that the whale is in state b during that interval.

(ii) Let γ_b be the probability that a whale in state b now, is still in state b in the next time interval.

(iii) Let γ_a be the probability that a whale in state a now, is still in state a in the next time interval.

Following MacDonald and Zucchini (1997), the likelihood for the sequence of click counts in the J intervals, $m_1, \ldots, m_J$ from a single whale is

$$L^*(\underline{\lambda}, \underline{\gamma}) \quad = \quad \underline{\delta}(\underline{\gamma}) \left(\prod_{j=1}^{J} \boldsymbol{B}(m_j; \underline{\lambda}, \underline{\gamma}) \right) \underline{1}^T \tag{3}$$

where $\underline{1} = (1,1)$, $\underline{\gamma} = (\gamma_a, \gamma_b)$,

$$\underline{\delta}(\underline{\gamma}) = \left(\frac{\gamma_a}{\gamma_a + \gamma_b}, \frac{\gamma_b}{\gamma_a + \gamma_b} \right) \tag{4}$$

and

$$\boldsymbol{B}(m_j; \underline{\lambda}, \underline{\gamma}) = \begin{pmatrix} 0 & \gamma_b, \pi_b(0; \underline{\lambda}) \\ 0 & (1-\gamma_b)\pi_b(0; \underline{\lambda}) \end{pmatrix} \quad \text{if } m_j = 0, \text{ while} \tag{5}$$

$$\boldsymbol{B}(m_j; \underline{\lambda}, \underline{\gamma}) = \begin{pmatrix} 1-\gamma_a & \gamma_b, \pi_b(m_j; \underline{\lambda}) \\ \gamma_a & (1-\gamma_b)\pi_b(m_j; \underline{\lambda}) \end{pmatrix} \quad \text{if } m_j > 0 \tag{6}$$

2.3 *Click detection model*

The probability of detecting a click is assumed to be a function of radial distance r of the click from the hydrophone, and other observable variables $\underline{z}$. For example, assuming half-normal detection function shape, and that $\underline{z}$ affects only the scale parameter:

$$p(r, \underline{z}; \underline{\beta}) = \exp\left\{ \frac{-r^2}{2\exp\left\{\beta_0 + \underline{\beta}'_z \underline{z}\right\}^2} \right\} \tag{7}$$

where $\underline{\beta}$ is the vector of detection function parameters.

If the click process pdf in (i) above is Poisson with rate parameter $\underline{\lambda} = \lambda$ (i.e. $\pi_b(m \mid \lambda) = e^{-\lambda}\lambda^m/m!$), the locations of clicks occurring in interval j is a nonhomogeneous Poisson process with rate parameter $p(r_{\nearrow}, \underline{z}; \underline{\beta})\lambda$, where $r_{\nearrow}$ indicates the radial distance path taken by the whale in the interval. This is approximated here by a homogeneous Poisson process with rate parameter

$p(\bar{r}_j, \underline{z}; \underline{\beta})\lambda$, where $\bar{r}_j$ is the mean radial distance of an animal in the jth interval.

2.4 *Likelilhood for observations from a single whale*

With the Poisson assumption and approximation of the previous paragraph, the pdf of the **observed** sequence of click counts in interval j, given that an animal is in state b, is modelled as a Poisson random variable with rate parameter$p(\bar{r}_j, \underline{z}; \underline{\beta})\lambda$. That is, $\pi_b(n_j \mid \lambda, \underline{\beta}, \bar{r}, \underline{z})= e^{-\lambda p(\bar{r}_j, \underline{z}; \underline{\beta})}(\lambda p(\bar{r}_j, \underline{z}; \underline{\beta}))_j^n/n_j!$. The likelihood for $\underline{\lambda}, \underline{\gamma}$ and $\underline{\beta}$ given the observed counts $\underline{n} = (n_1, \ldots, n_J)$, mean radial distances $\underline{\bar{r}} = (\bar{r}_1, \ldots, \bar{r}_J)$ and $\underline{z}$ then has same form as Equation (3) above, and can be written as

$$L_{\underline{n}}(\underline{\lambda}, \underline{\gamma}, \underline{\beta} \mid \underline{\bar{r}}) \quad = \quad \underline{\delta}(\underline{\gamma}) \left(\prod_{j=1}^{J} \boldsymbol{B}(n_j; \underline{\lambda}, \underline{\gamma}, \underline{\beta}) \right) \underline{1}^T \qquad (8)$$

Now consider whale w: its mean radial distance in each of the J intervals, $\underline{\bar{r}}_w$ is a deterministic function of the whale's location (x_w, y_w) and the set of predefined intervals indexed $j = 1, \ldots, J$. Hence we write $\underline{\bar{r}}_w$ as $\underline{\bar{r}}(x_w, y_w)$. This can be estimated from Equation (1) evaluated over the set of click segments $\{i\}_w$ from whale w:

$$L_{\underline{b}}(\underline{\bar{r}}(x_w, y_w), \underline{\kappa}) \quad = \quad \prod_{i \in \{i\}_w} f_{\underline{b}}(\underline{b}_i \mid \underline{t}_i, x_w, y_w, \underline{\kappa}) \qquad (9)$$

The joint likelihood for whale location $\underline{\bar{r}}(x_w, y_w)$ and the parameters $\underline{\lambda}$, $\underline{\gamma}$, $\underline{\beta}$ and $\underline{\kappa}$ using data $\underline{n}_w$ and $\underline{b}_w$ from whale w alone is therefore

$$L_w(\underline{\lambda}, \underline{\gamma}, \underline{\beta}, x_w, y_w, \underline{\kappa}) \quad = \quad L_{\underline{n}_w}(\underline{\lambda}, \underline{\gamma}, \underline{\beta} \mid \underline{\bar{r}}(x_w, y_w)) L_{\underline{b}_w}(\underline{\bar{r}}(x_w, y_w), \underline{\kappa}) \quad (10)$$

2.5 *Likelihood for all detected whales*

Let $\mathcal{G}(N_{obs})$ be a particular grouping of observed click segments into N_{obs} sets, one from each of N_{obs} whales. Given $\mathcal{G}(N_{obs})$, the likelihood for the above parameters is

$$L_{\mathcal{G}(N_{obs})}(\underline{\lambda}, \underline{\gamma}, \underline{\beta}, \underline{x}, \underline{y}, \underline{\kappa}) = \prod_{w=1}^{N_{obs}} L_w(\underline{\lambda}, \underline{\gamma}, \underline{\beta}, x_w, y_w, \underline{\kappa}) \qquad (11)$$

where $\underline{x} = (x_1, \ldots, x_{N_{obs}})$ and $\underline{y} = (y_1, \ldots, y_{N_{obs}})$.

Let $\mathcal{S}\{\mathcal{G}(N_{obs})\}$ be the set of all possible combinations of the observed click segments into observed click histories from N_{obs} individual whales. The likelihood for N_{obs} (and other parameters) is

$$L(N_{obs}, \underline{\lambda}, \underline{\gamma}, \underline{\beta}, \underline{x}, \underline{y}, \underline{\kappa}) = \sum_{\mathcal{S}\{\mathcal{G}(N_{obs})\}} L_{\mathcal{G}(N_{obs})}(\underline{\lambda}, \underline{\gamma}, \underline{\beta}, \underline{x}, \underline{y}, \underline{\kappa}) \qquad (12)$$

2.6 *Density estimation: line transect approach*

Given estimates of N_{obs}, $\underline{\lambda}$, $\underline{\gamma}$ and $\underline{\beta}$ from maximizing Equation (12), density and abundance can be estimated using a Horvtiz-Thompson-like estimator:

$$\hat{D} = \frac{1}{a} \sum_{w=1}^{\hat{N}_{obs}} \frac{1}{\hat{p}(\underline{z}_w)} \qquad (13)$$

Here $\hat{p}(\underline{z}_w) = \int_0^{x_W} \hat{p}(x, \underline{z}_w) \frac{1}{x_W}$ and x_W is the maximum observed x. The probability $\hat{p}(x, \underline{z}_w)$ could be obtained by $1 - \prod_{\{j(x)\}} \widehat{\Pr}\{n_j > 0 \mid x\}$ where $\{j(x)\}$ is the set of intervals at perpendicular distance x between the angles θ_{min} and θ_{max}, and

$$\widehat{\Pr}\{n_j > 0 \mid x\} = \frac{\hat{\gamma}_b}{\hat{\gamma}_a + \hat{\gamma}_b} \left[1 - \pi_b(0 \mid \hat{\lambda}, \underline{\hat{\beta}}, \bar{r}_j(x), \underline{z})\right] \tag{14}$$

and $\bar{r}(x)$ is the mean radial distance of the jth interval in $\{j(x)\}$.

This is very messy and complicated!!

An alternative is to use $\hat{N}_{obs}$ only to estimate mean school size, and to use conventional line transect methods on schools to estimate school abundance. If schools are readily identifiable (using some pre-defined criteria) and detection probability does not depend on school size, this seems OK to me - although it is hardly elegant. Details to be worked out.

2.7 *Density estimation: cue-counting-like approach*

From Equation (12) we get MLEs of the click production model parameters $\underline{\lambda}$ and $\underline{\gamma}$, and the detection function parameters $\underline{\beta}$. Hence we have an estimate of the mean click rate per interval:

$$\hat{E}[n] = \left(\frac{\hat{\gamma}_b}{\hat{\gamma}_a + \hat{\gamma}_b}\right) \hat{\lambda} \tag{15}$$

and assuming intervals to be defined to be of equal time length τ say, we have an estimate of mean click rate: $\hat{E}[n]/\tau$.

We also have an estimate of the radial distance detection function $p(r, \underline{z})$, and hence we could use the cue-counting estimator described in Section 3.4. So why go this more complicated route rather than use the method described in Section 3? Well, the advantages of this method are:

- In principle, you get an estimate of the mean click rate from this survey, and by bootstrapping (on transects say) you get an estimate of the variance of the density or abundance estimator which includes variance due to mean click rate. This could be a big plus, since (a) mean cue rate estimation is usually difficult and possibly biased because it is seldom done in the same place (and never the same time) as the survey, and (b) estimating its variance is usually well-nigh impossible and is neglected.

- At worst, you can specify $\underline{\gamma}$ and λ - and then you're down to the method of Section 3.

3. Cue-counting approach

(NOTE: notation in this section is a bit inconsistent with that above.) A cue-counting approach sidesteps the problem of having to model the full cue generation process, requiring only the mean cue rate and its variance. The cost of the reduction in complexity comes in having to estimate this mean and variance. If they are not estimated in the same place at the same time as the cue-counting survey, they may be inappropriate for that population and inferences may be biased.

3.1 *Bearing observation model*

It is convenient to reformulate the bearing observation model in polar coordinates for the cue-counting likelihood. We use the same notation as in Section 2.1 except that we work in terms of (r_{ic}, θ_{ic}), the radial distance and angle from the hydrophone to the cth click from the $i$the click segment ($i = 1, \ldots, I$; $c = 1, \ldots, C_i$). We assume that whales are stationary for the duration of each click segment, so that (r_{ic}, θ_{ic}) is a deterministic function of r_{1c}, θ_{1c}, t_{1c} and t_{ic}, as follows:

$$
\begin{aligned}
r_{ic} &= r_{ic}(r_{1c}, \theta_{1c}, t_{1c}, t_{ic}) &=& \sqrt{r_{1c}^2 + (v\delta t_{ic})^2 - 2r_{1c}v\delta t_{ic}\cos(90 - \theta_{1c})} && (16)\\
\theta_{ic} &= \theta_{ic}(r_{1c}, \theta_{1c}, t_{1c}, t_{ic}) &=& \tan^{-1}\left(\frac{r_{1c}\sin(\theta_{1c}) - v\delta t_{ic}}{r_{1c}\cos(\theta_{1c})}\right) && (17)
\end{aligned}
$$

where $\delta t_{ic} = t_{ic} - t_{1c}$ and v is the speed of the hydrophone. See Figure 3

[Figure 3 about here.]

Let $f_b(b_{ic} \mid r_{ic}, \theta_{ic}; \underline{\kappa})$ be the probability density function for the cth measured bearing b_{ic} in segment i, given the source of the clicks, (r_{ic}, θ_{ic}), with parameter vector $\underline{\kappa}$. Let $f_{\underline{b}}(\underline{b}_i \mid \underline{r}_i, \underline{\theta}_i; \underline{\kappa})$ be the joint probability density function for the C_i measured bearings $\underline{b}_i = (b_{i1}, \ldots, b_{iC_i})$ from the $i$the segment, given the source of the clicks, $\underline{r}_i = (r_{i1}, \ldots, r_{iC_i})$, $\underline{\theta}_i = (\theta_{i1}, \ldots, \theta_{iC_i})$. With independent detections,

$$
\begin{aligned}
f_{\boldsymbol{b}}(\boldsymbol{b} \mid \boldsymbol{t}, \underline{r}, \underline{\theta}, \underline{\kappa}) &= \prod_{i=1}^{I} f_{\underline{b}}(\underline{b}_i \mid \underline{b}_i, \underline{r}_i, \underline{\theta}_i, \underline{\kappa}) \\
&= \prod_{i=1}^{I}\prod_{c=1}^{C_i} f_b(b_{ic} \mid b_{ic}, r_{ic}, \theta_{ic}, \underline{\kappa}) \qquad (18)
\end{aligned}
$$

3.2 *Detection function*

We consider estimation for the case in which data are truncated at radial distance r_W and angles $-\theta_W$ radians and θ_W radians.

Let $p(r, \underline{z}; \underline{\beta})$ be the probability of detecting a click made at radial distance r from the hydrophone, given associated variables $\underline{z}$ and parameter vector $\underline{\beta}$. (We assume detection probability to be independent of angle.) Let $\pi_1(r, \theta)$ be the pdf of the location of the first click in a segment. Given the times $\underline{t}_i$

of the C_i detected clicks from the ith segment, the joint pdf of their radial distances $\underline{r}_i$ and the angle of the first detection θ_{i1}, is therefore

$$f_{\underline{r}}(\underline{r}_i, \theta_{i1} \mid \underline{t}_i; \underline{\beta}) = \frac{\prod_{c=1}^{C_i} p(r_{ic}, \underline{z}_{ic}; \underline{\beta}) \pi_1(r_{i1}, \theta_{i1})}{\int_{\theta_{min}}^{\theta_{max}} \int_0^{r_W} \prod_{c=1}^{C_i} p(r_{ic}, \underline{z}_{ic}; \underline{\beta}) \pi_1(r_{i1}, \theta_{i1})\, dr_{i1}\, d\theta_{i1}} \tag{19}$$

where r_{ic} is given by Equation (16) and $\pi_1(r_{i1}, \theta_{i1}) = r_{i1}/[r_W^2(\theta_{max} - \theta_{min})]$. If we consider only the initial radial distance, r_{i1}, the relevant likelihood is

$$f_{r_1}(r_{i1}, \theta_{i1} \mid \underline{t}_i; \underline{\beta}) = \frac{p(r_{i1}, \underline{z}_{i1}; \underline{\beta}) \frac{r_{i1}}{(\theta_{max} - \theta_{min})}}{\int_0^{r_W} p(r, \underline{z}_{i1}; \underline{\beta}) r\, dr} \tag{20}$$

3.3 *The likelihood function*

Using Equations (18) and (19), we can then write the likelihood for the parameters $\underline{\beta}$ of the detection function $p(r, \underline{z}; \underline{\beta})$ and the parameters $\underline{\kappa}$ of the observation error model $f_{\underline{b}}(\underline{b}_i \mid \underline{r}_i, \underline{\theta}_i; \underline{\kappa})$, given detections at bearings $\boldsymbol{b}$ at times $\boldsymbol{t}$, as follows:

$$\begin{aligned} L(\underline{\beta}, \underline{\kappa} \mid \boldsymbol{b}, \boldsymbol{t}) &= \prod_{i=1}^{I} L_i(\underline{\beta}, \underline{\kappa} \mid \underline{b}_i, \underline{t}_i) \qquad (21) \\ &= \prod_{i=1}^{I} \int_{\theta_{min}}^{\theta_{max}} \int_0^{r_W} f_{\underline{r}}(\underline{r}_i, \theta_{i1} \mid \underline{t}_i; \underline{\beta}) f_{\underline{b}}(\underline{b}_i \mid \underline{r}_i, \underline{\theta}_i; \underline{\kappa})\, dr_{i1}\, d\theta_{i1} \end{aligned}$$

3.4 *The whale abundance estimator*

Since data are truncated at radial distance r_W and angles θ_{min} radians and θ_{max} radians, an area $a = \gamma \pi r_W^2$ about the hydrophone is searched, where $\gamma = \theta_W / \pi$. Suppose also that the hydrophones search for time T_k on the Kth transect, from which I_k click segments are detected ($k = 1, \ldots, K$) and that there are C_{ki} clicks in the $i$the click segment on the kth transect, the cth of which has associated variables $\underline{z}_{kic}$.

We estimate the density of cues per unit time by

$$\hat{D}_{click} = \sum_{k=1}^{K} \sum_{i=1}^{I_k} \frac{1}{\hat{p}(\boldsymbol{z}_{ki}) T_k a} \tag{22}$$

where $\boldsymbol{z}_{ki} = (\underline{z}_{ki1}, \ldots, \underline{z}_{kiC_{ki}})$ and

$$\hat{p}(\boldsymbol{z}_{ki}) = \int_{\theta_{min}}^{\theta_{max}} \int_{0}^{r_W} \prod_{c=1}^{C_i} p(r_{ic}, \underline{z}_{ic}; \underline{\beta}) \pi_1(r_{i1}, \theta_{i1})\, dr_{i1}\, d\theta_{i1} \tag{23}$$

Here r_{ic} is given by Equation (16) and $\pi_1(r, \theta) = r/[r_W^2(\theta_{max} - \theta_{min})]$. The resulting estimator of animal abundance is

$$\hat{N} = \frac{\hat{D}_{click}}{\hat{\lambda}} A \tag{24}$$

where A_s is the surface area of the study region and $\hat{\lambda}$ is an estimate of the mean cue rate - the mean number of cues produced per animal per time unit.

3.4.1 Variance estimation Variance is estimated by nonparametric bootstrap using the transects as the resampling unit.

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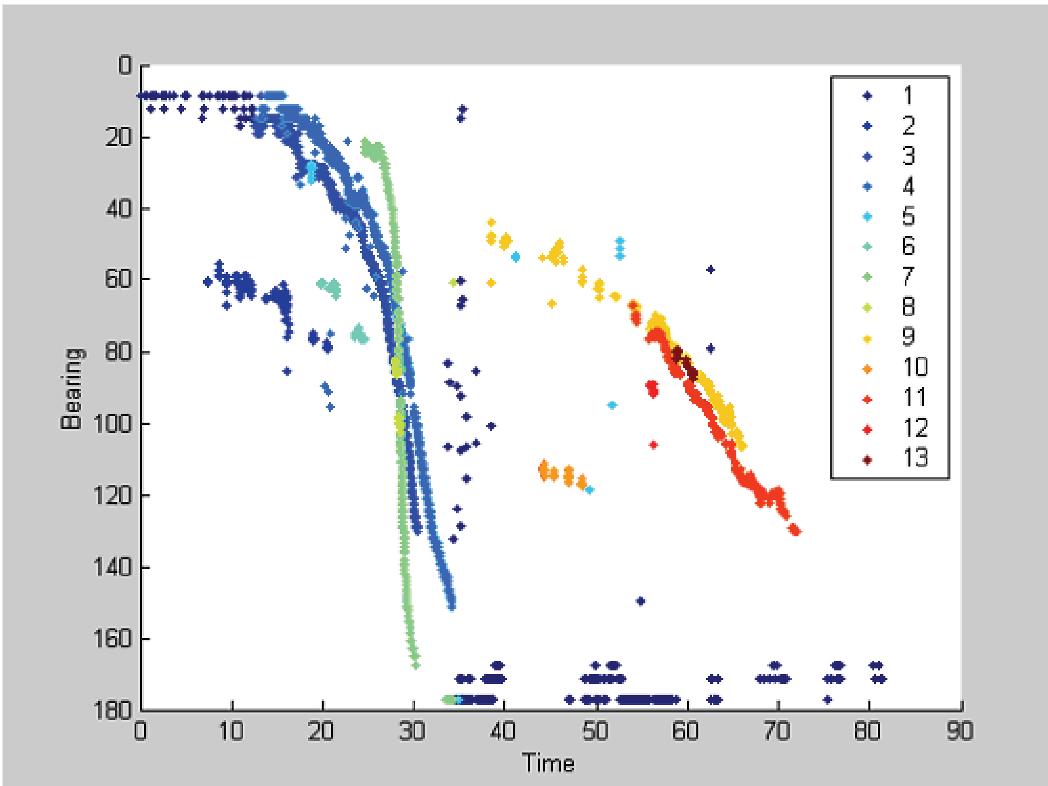

Figure 1. An example of data. Segments of clicks judged to be from the same whale are coloured the same; the key shows the colours of each numbered segment.

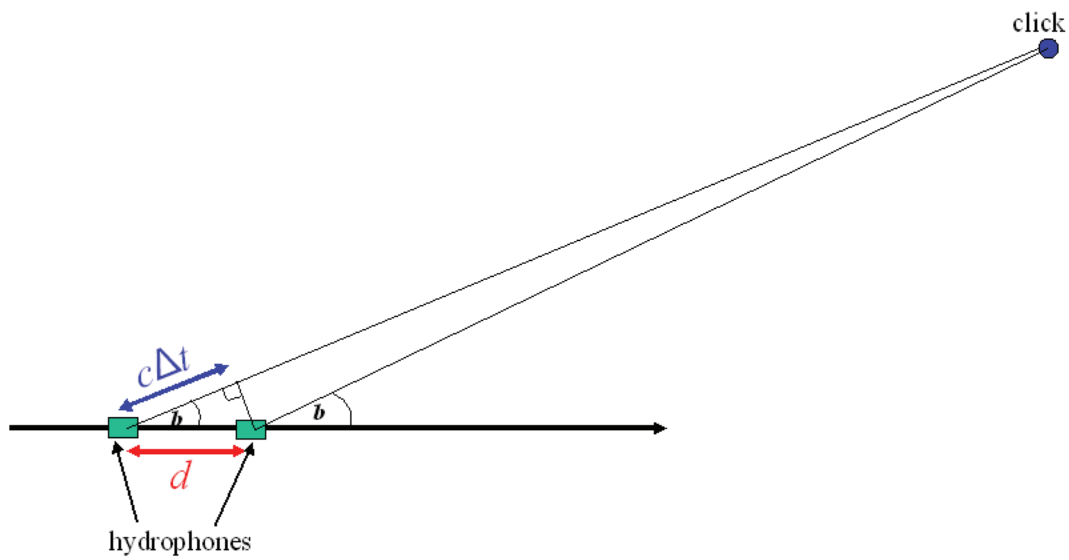

Figure 2. The basis of the angle (b) calculation, as a function of Δt, the time between the arrival of a click at the first and second hydrophones, the distance between the hydrophones, d, and the speed of sound in water, c. Clicks are assumed to far enough away that the angles b at the two hydrophones can be treated as equal.

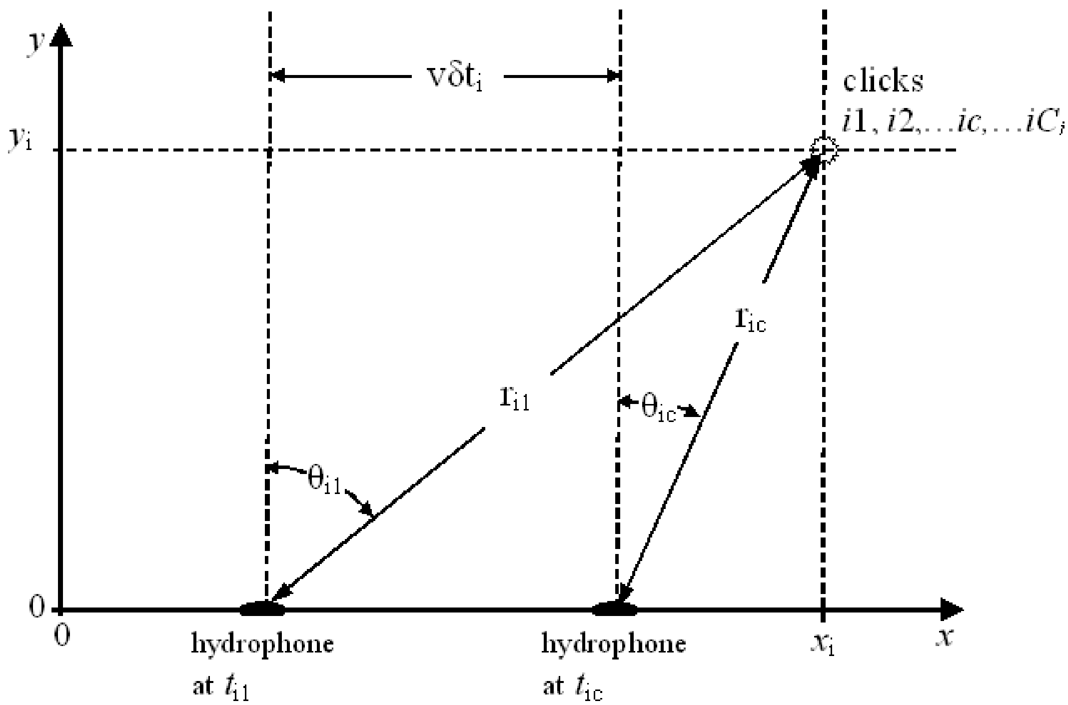

Figure 3. Notation for the *ith* click segment.